

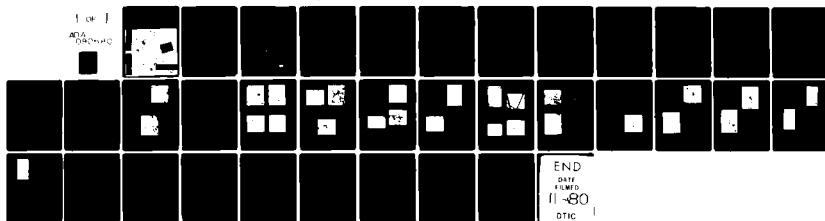
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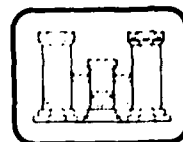
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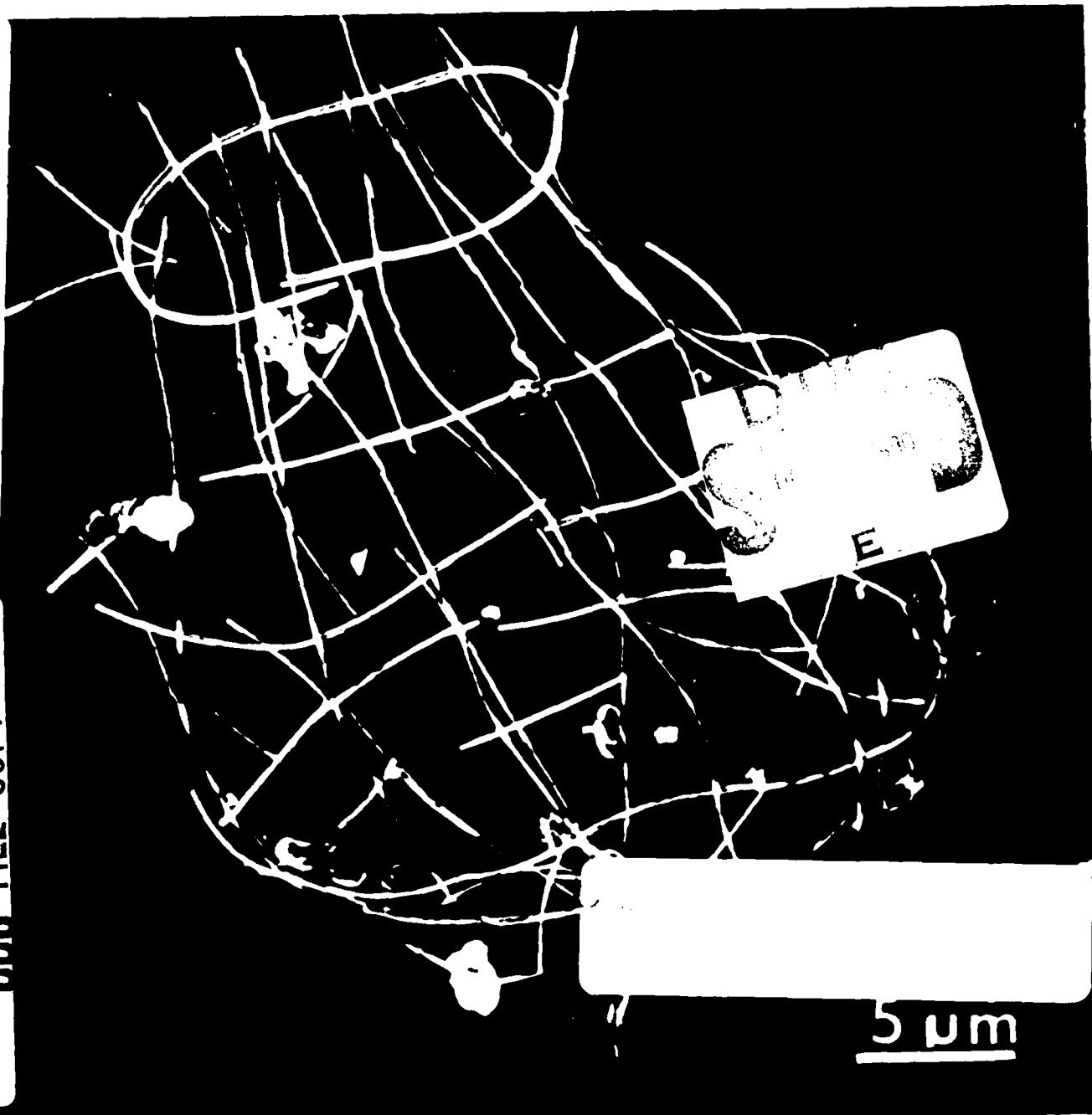
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*Morphology and distribution of the Acanthoecidae
(Choanoflagellata) from the Weddell Sea during the
austral summer, 1977*

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*Cover: Scanning electron micrograph (approx. $\times 5500$) of *Diaphanoeca multiannulata* sp. nov. from pond on ice floe in Weddell Sea.*

CRREL Report 80-16

Morphology and distribution of the Acanthoecidae (Choanoflagellata) from the Weddell Sea during the austral summer, 1977,

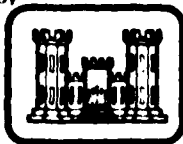
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REPORT DOCUMENTATION PAGE		READ INSTRUCTIONS BEFORE COMPLETING FORM
1. REPORT NUMBER CRREL Report 80-16	2. GOVT ACCESSION NO. AD-A090680	3. RECIPIENT'S CATALOG NUMBER
4. TITLE (and Subtitle) MORPHOLOGY AND DISTRIBUTION OF THE ACANTHOECIDAE (CHOANOFLLAGELLATA) FROM THE WEDDELL SEA DURING THE AUSTRAL SUMMER, 1977		5. TYPE OF REPORT & PERIOD COVERED
7. AUTHOR(s) Kurt Buck		6. PERFORMING ORG. REPORT NUMBER
9. PERFORMING ORGANIZATION NAME AND ADDRESS U.S. Army Cold Regions Research and Engineering Laboratory Hanover, New Hampshire 03755		8. CONTRACT OR GRANT NUMBER(s) National Science Foundation Grant DPP76-15251 and DPP76-80738
11. CONTROLLING OFFICE NAME AND ADDRESS National Science Foundation Washington, D.C.		10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS
14. MONITORING AGENCY NAME & ADDRESS (if different from Controlling Office)		12. REPORT DATE July 1980
		13. NUMBER OF PAGES
		15. SECURITY CLASS. (of this report) Unclassified
		15a. DECLASSIFICATION/DOWNGRADING SCHEDULE
16. DISTRIBUTION STATEMENT (of this Report) Approved for public release; distribution unlimited.		
17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)		
18. SUPPLEMENTARY NOTES		
19. KEY WORDS (Continue on reverse side if necessary and identify by block number) Antarctic regions Sea Ice Choanoflagellates Taxonomy Ocean environments Plankton		
20. ABSTRACT (Continue on reverse side if necessary and identify by block number) Eight species of loricate choanoflagellates (<i>Acanthoecidae</i>), <i>Acanthoecopsis spiculifera</i> , <i>Bicosta spinifera</i> , <i>Bicosta antennigera</i> , <i>Calliicantha simplex</i> , <i>Calliicantha multispina</i> aff., <i>Crinolina aperta</i> , <i>Diaphanoeca multiannulata</i> , and <i>Parvicorbicula socialis</i> , were observed in samples obtained from the Weddell Sea during the austral summer, 1977. <i>D. multiannulata</i> was described for the first time from these samples; the other organisms have either been described previously or are being described at this time. The distribution of most species within the Weddell Sea was widespread. The distributional, environmental, and morphological range of <i>A. spiculifera</i> , <i>B. spinifera</i> , <i>C. aperta</i> , and <i>P. socialis</i> was expanded. Habitats in which choanoflagellates were found included the water column, the edges of ice floes, ponds on		

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20. Abstract (cont'd)

ice floes, and the interiors of ice floes. The presence of choanoflagellates within the ice indicates that there may be a closely coupled trophic relationship with the other two biological components of the ice community, the ice algae and the bacteria. The presence in the ice of seven species with both a caudal appendage and anterior projections suggests a positive relationship between this lorica configuration and the ice habitat. Mechanisms of variance of transverse costal diameters between genera may be useful to the taxonomy and phylogeny of this family.

7

PREFACE

This report was prepared by Kurt Buck, Biological Technician, Snow and Ice Branch, Research Division, U.S. Army Cold Regions Research and Engineering Laboratory. The author gratefully acknowledges the guidance, support, and inspiration of Dr. Sayed El-Sayed, Dr. Greta Fryxell, Dr. Nestor Bottino, and Dr. Saturo Taguchi. S. Ackley, M. Meyer, R. Warner, and the crew and officers of the USCG Icebreaker *Burton Island* assisted in making the field collections. The author also appreciates the assistance of H. Thomsen, I. Manton, Ø. Moestrup, R. Norris, S. Eubanks, and M. Hoban who supplied inspiration, technical assistance, and critical reviews during the preparation of this report. The collection program was funded by National Science Foundation Grants DPP76-15251 to U.S. Army Cold Regions Research and Engineering Laboratory and DPP76-80738 to Texas A&M University. The analysis was funded by the Smithsonian Oceanographic Center Cooperative Systematics Program, National Science Foundation Grant 76-23979.

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MORPHOLOGY AND DISTRIBUTION OF THE ACANTHOECIDAE (CHOANOFLLAGELLATA) FROM THE WEDDELL SEA DURING THE AUSTRAL SUMMER, 1977

Kurt Buck

INTRODUCTION

Literature review

The placement of choanoflagellates as a group in either the plant or animal kingdom has vacillated back and forth for a century. Based upon mitochondrial and flagellar substructure (Leadbeater and Manton 1974, Hibberd 1975, 1976), these organisms are now assigned to the Families Codonosigidae, Salpingoecidae and Acanthoecidae, Order Choanoflagellata, Class Zoomastigophorea, Phylum Protozoa. The cells of the Family Codonosigidae are naked, the cells of the Family Salpingoecidae are thecate (bounded by an investment without costae), and the cells of the Family Acanthoecidae are loricate (bounded by an investment with costae made of siliceous strips) (Leadbeater 1977, Norris 1965). The Acanthoecidae are further differentiated from the other choanoflagellates in that they are exclusively marine. This study will concern itself with the Acanthoecidae.

With the erection of the genera *Crinolina* (Thomsen 1976), *Bicosta* (Leadbeater 1978), and *Calliacantha* (Leadbeater 1978), there are now approximately 12 genera and 40 species which belong to the Family Acanthoecidae. Geographically, loricate choanoflagellates have been found in polar (Manton et al. 1975, Throndsen 1970a,b, Reynolds 1976, Deflandre 1960, Manton and Oates 1979b), temperate (Leadbeater 1972a, b, 1973, Manton and Oates 1979a, Moestrup 1979, Norris 1965, Thomsen 1973, 1976, 1977, Throndsen 1969, 1974), subtropical (G. Fryxell pers. comm.), and tropical (Manton and Oates 1979b) regions. With the exception of Deflandre's report from Terre Adelie of *Parvicorbicula socialis* (Meunier) Deflandre, a seemingly cosmo-

politan species, the polar reports have been primarily of arctic species.

As a group choanoflagellates seem to favor calm waters of nearshore areas for their habitat, being found in the stagnant water of salt marshes (Leadbeater and Morton 1974a), tide pools (Norris 1965), fjords (Throndsen 1974, Thomsen 1973, 1976) and coastal waters (Throndsen 1969, Manton et al. 1975, 1976). Observations in open ocean have been made on two species of the genus *Bicosta* (Throndsen 1970b, Reynolds 1976). Neustonic (Norris 1965), epiphytic (Ellis 1930, Norris 1965), and planktonic (Throndsen, 1974) modes of existence have been described. Manton et al. (1975) propose an association with sea ice as a common denominator for a group of Acanthoecidae observed in the Canadian Arctic, although no specific reports of such an association were made. The presence of at least one species under arctic sea ice has been documented (Manton and Oates 1979b). Environmental tolerances of the family as a whole seem to be wide; they have been found in water with temperatures ranging from -1°C to 24°C and salinities ranging from 5‰ to 36‰. Without exception, insufficient data exist to be able to establish habitat, environmental, or geographical ranges for any given species.

In describing the morphology of the Family Acanthoecidae the terminology of Leadbeater (1972a) will be followed. The lorica is composed of longitudinal and transverse costae (Fig. 1). The anterior end is open (the posterior end in *Crinolina* spp. is open as well) and has the flagellum projecting from it. In the present taxonomic scheme the lorica shape, presence or absence of anterior projections, numbers of costae (both longitudinal and transverse), and in one case the

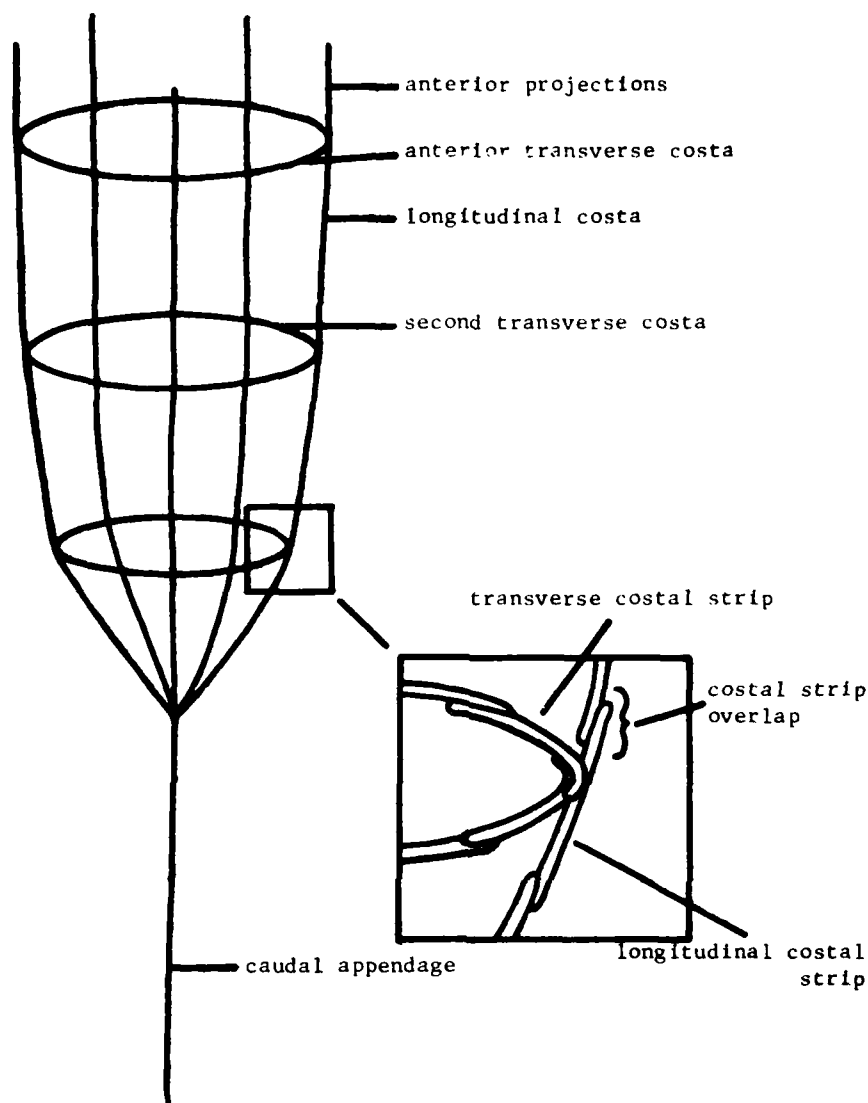


Figure 1. Morphology of Acanthoecidae.

orientation of the costae (*Acanthoeca* Ellis) are characteristics most commonly used to differentiate genera. Costal numbers (both longitudinal and transverse), presence or absence of a caudal appendage, and costal shape are the characteristics most commonly used to differentiate species. Each costa is made up of rod shaped subunits, called costal strips, which in some species are heteropolar. The heteropolar costal strips are tapered at one end and bulbous, T-shaped, or L-shaped at the other end. Other costal strips are usually tapered at both ends. In the species that have heteropolar transverse

costal strips, it is the non-tapered end that is responsible for joining individual costal strips and connecting longitudinal and transverse costae. The variation of costal substructure between species has been largely ignored in the literature, making assessment of its taxonomic importance difficult. The shape and size of the protoplast, the length of the flagellum, and the number and length of the collar tentacles are characteristics that are usually included in a species description, but differentiation on both the generic and specific levels is based solely upon lorica morphology.

The composition of the costal strips and hence the lorica has been determined to be siliceous. Exposure to hydrofluoric acid (Leadbeater and Morton 1974b) and X-ray analysis (Thomsen 1973) have been used to test this. When tests for crystalline structure of the silicon were conducted and negative results obtained, Leadbeater and Manton (1974) concluded that the silicon was present in an amorphous form. The substance holding the costal strips to one another does not withstand treatment with potassium permanganate and hydrochloric acid, a procedure used to clean organic matter from diatom frustules (Fryxell and Hasle 1970), indicating that it may be organic in nature.

Bacteria and other small particles are ingested by choanoflagellates as food. Collar tentacles remove the particles from the water currents set up by the beating of the flagellum inside the lorica (Leadbeater and Morton 1974a, Ellis 1930), although presumably dissolved organic matter may also function as a food source for some species (Gold et al. 1970).

Reproduction (production of another protoplast) and replication (production of another lorica) have been studied with both light and electron microscopes, using wild as well as cultured organisms. The entire sequences have been established by piecing together discrete observations of the separate steps (Ellis 1930, Thomsen 1976, 1977, Leadbeater 1975). After reproduction occurs, the juvenile protoplast migrates out of the mother lorica and attaches to the external anterior end of the lorica, a position it usually maintains only for a short period of time (Thomsen 1977). Costal strip bundles are present within the juvenile cells (Leadbeater and Manton 1974); it is presumably these costal strips that are laid around the juvenile protoplast to produce a new lorica. All evidence points to an exact placement of specific costal strips (Manton et al. 1976) although the mechanism involved is still unknown. Thomsen (1973) has observed what could be interpreted as a mature lorica initiating division at its posterior end. Colony formation as a result of juvenile cells and loricas not dissociating themselves from the parent loricas has been observed. The colonies may be spherical (anterior ends directed inwards) (Thomsen 1976) or in mats (Detlandre 1960, Manton et al. 1976), depending upon the species and the interpretation.

Objectives

Determining the geographical, habitat, and

spatial distribution of selected species of the Acanthoecidae, particularly with respect to previous observations, is one of the main objectives of this report. Another objective is to examine the costal substructure of the species with a scanning electron microscope in an attempt to clarify the taxonomic importance of this characteristic. A new species, *Diaphanoeca multianulata*, is described for the first time from these samples.

MATERIALS AND METHODS

This study was essentially observational in nature, using standard methods of light and scanning electron microscopy. The morphological and taxonomic aspects of this study rely heavily upon micrographs of selected organisms from sampling stations where the concentrations were highest. The distributional aspect relies on surveying samples obtained during a cruise of the US Coast Guard icebreaker *Burton Island* to the Weddell Sea during February and March 1977 (Fig. 2, Table 1). Samples were obtained in three ways: with a 35 μ m mesh net towed from a depth of 200 m below the surface, with a CRRF ice corer that obtains a 7-cm-diameter cylinder through ice floes, and by hand from the edges of ice floes and from ponds on ice floes. A total of thirty-three water column and five ice floe samples were taken (Table 1) and examined. Of the five ice samples, four were obtained from ice floe edges or ponds and one was obtained with the ice corer.

Samples were preserved as soon as possible after collection with enough hexamine-buffered formalin to produce a concentration of approximately 2% formalin in the sample. The samples were returned to Texas A&M University for subsequent analysis. Approximately 20 ml from each sample was rinsed with laboratory distilled water using a centrifugation-decantation technique (the sample is centrifuged, the supernatant decanted, and distilled water added). After the final (fourth) rinse a pipette was used to transfer a portion of the pellet to whole coverslips for use with the light microscope (LM) or to a portion of a cleaned coverslip mounted on an aluminum stub for use with the scanning electron microscope (SEM). The samples were then air dried. Those samples to be studied with the light microscope were covered with Hyrax or Cumar (mounting media) and allowed to dry overnight; the excess mounting medium was then scraped

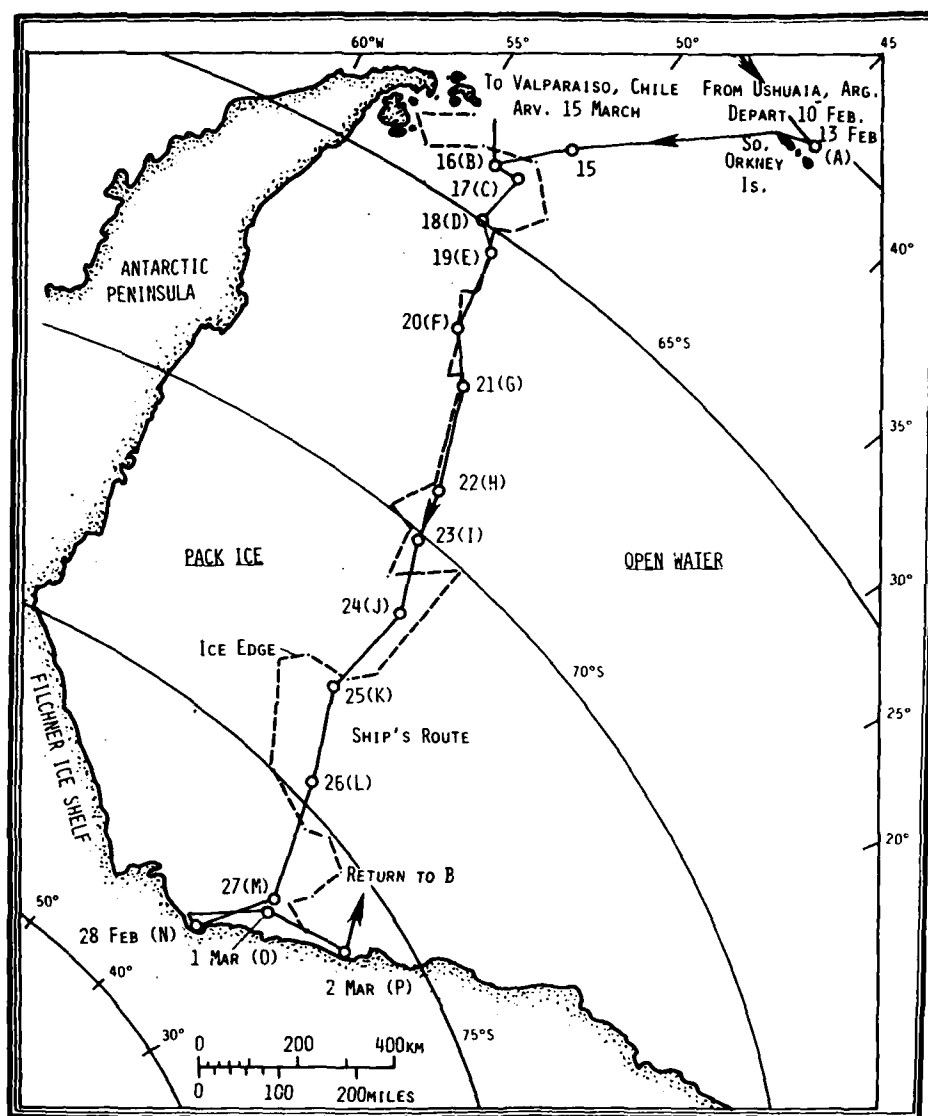


Figure 2. Cruise track and pack ice limits of the Weddell Sea biocruise, February-March 1977. Dashed line represents the pack ice limit and the solid line represents the cruise track.

away and the edges were sealed with fingernail polish. The samples for the SEM were grounded to the stub with silver paint and coated with gold-palladium. The light microscope was a Zeiss Standard K with phase optics; the scanning microscopes used were Hitachi JSM U-3 and U-35.

RESULTS

Observations

Diaphanoeca multiannulata sp. nov. Figs 3-12
 Diagnosis: Torus barrel shaped. Transverse costae, 4 or 5 composed of 11-13 costal strips, bulbous at one end, tapered at other end, spaced

Table 1. Location, date, type of sample, surface temperature, and salinity of the stations occupied during the Weddell Sea biocruise, February-March 1977.

Sta.	Latitude (S)	Longitude (W)	Date (1977)	Sample type	Surface temp (°C)	Surface sal. (‰)
A	60°17.0'	44°34.0'	13 Feb	Net	1.7	34.1
B	63°57.0'	53°12.0'	16 Feb	Net	1.7	33.4
B-C	63°56.0'	52°13.0'	17 Feb	Ice*		
B-C	63°58.0'	52°25.0'	17 Feb	Net		
C	63°58.0'	52°25.0'	17 Feb	Net	0.8	33.2
C-D	64°13.0'	51°56.0'	18 Feb	Net		
D	64°57.6'	56°26.2'	18 Feb	Ice*		
D	64°57.6'	56°26.2'	18 Feb	Net	1.7	34.3
D-E	65°13.0'	51°51.0'	19 Feb	Net		
E	65°23.0'	51°28.0'	19 Feb	Ice*		
E	65°23.0'	51°28.0'	19 Feb	Net	1.7	
E-F	65°59.6'	51°42.3'	19 Feb	Net		
F	66°45.1'	50°30.5'	20 Feb	Net	-1.3	33.8
F-G	67°04.5'	50°00.0'	20 Feb	Net		
G	67°49.4'	49°07.2'	21 Feb	Net	-0.8	33.3
G-H	68°43.0'	47°28.0'	21 Feb	Net		
H	69°21.0'	46°46.0'	22 Feb	Net	1.7	33.5
H-I	69°30.0'	46°55.0'	22 Feb	Net		
I	70°15.2'	45°36.8'	23 Feb	Ice*		
I	70°15.2'	45°36.8'	23 Feb	Net	2.2	33.4
I-J	70°39.0'	44°00.0'	23 Feb	Net		
J	71°25.0'	45°00.0'	24 Feb	Net	1.6	33.7
J-K	72°08.0'	41°35.5'	24 Feb	Net		
K	73°07.0'	41°44.0'	25 Feb	Ice†		
K	73°07.0'	42°44.0'	25 Feb	Net	1.5	33.4
K-L	74°08.0'	41°08.0'	25 Feb	Net		
L	74°37.6'	38°54.8'	26 Feb	Net	1.9	33.4
L-M	74°41.1'	36°32.3'	26 Feb	Net		
M	75°39.5'	34°27.0'	27 Feb	Net	-2.0	34.0
M-N	77°27.0'	34°54.0'	27 Feb	Net		
N	77°46.0'	35°10.0'	28 Feb	Net	-2.4	33.8
N-O	77°46.0'	35°59.0'	28 Feb	Net		
O	76°54.6'	34°04.1'	1 Mar	Net	-1.3	33.8
O-P	76°49.7'	32°27.9'	1 Mar	Net		
P	76°19.8'	28°40.0'	2 Mar	Net	-1.7	33.3

*Ice floe pond or edge
†Ice floe core

at intervals of 1-1/2, 4, 5-1/2, and 7 costal strips from anterior ends of longitudinal costae; longitudinal costae 11-13, composed of 8-9 costal strips, blunt at both ends, of slightly smaller diameter than transverse costal strips, projections 1-1/2 costal strips in length occurring beyond anterior costa; caudal appendage 3 costal strips in length arising from reduction and convergence of longitudinal costae posterior to 4th transverse costa.

Holotype: Figure 3.

Type location: 70°15.2'S, 45°36.8'W, 23/02/77, ice floe pond, -1.8°C.

Loricas of this species were found in many of the net tows and in four of the five ice samples

(Table 2). Although the number of costae varied (Figs. 4-6), twelve longitudinal and four transverse costae was the norm (Figs. 4, 5). Electron microscopy of this organism permitted the structure of the costae to be discerned. The transverse costae are composed of as many costal strips as there are longitudinal costae. The costal strips, bulbous on one end and blunt on the other end, are attached to the longitudinal costae by their bulbous ends and to each other by the blunt end somewhere along the adjoining costal strip (Fig. 6). The point of attachment for the blunt end and the adjoining costal strip differs for each costa; in the anterior transverse

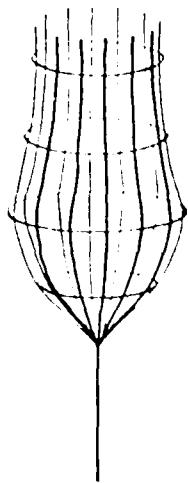


Figure 3 *Diaphanoeca multiannulata*. Line drawing

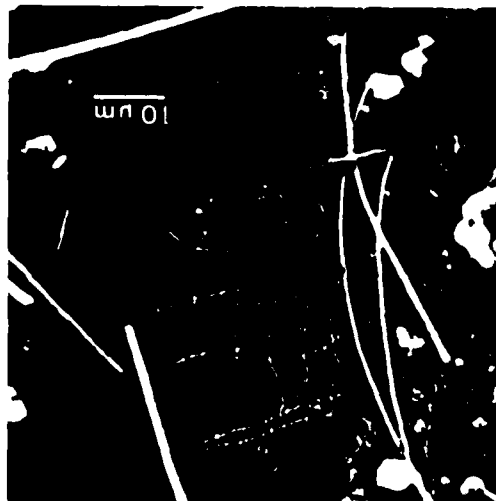


Figure 4 *Diaphanoeca multiannulata*. Intact loriciferous structure with caudal appendage. 4 transverse and 13 longitudinal costae. TM: Ice flow pond, station 1.



Figure 5 *Diaphanoeca multiannulata*. Loriciferous structure with 5 transverse costae (arrows). TM: Ice flow pond, station 1.

Table 2. Distribution of Acanthoecidae from the Weddell Sea biocruise, February-March 1977.

(I) denotes ice

Station	<i>Acanthoecopsis spiculifera</i>	<i>Bicosta antennigera</i>	<i>Bicosta spinifera</i>	<i>Calliacantha multispina</i>	<i>Calliacantha simplex</i>	<i>Crinolina aperta</i>	<i>Diaphanoeca multiannulata</i>	<i>Parvicorbicula socialis</i>
A								
A-B								
B							X	
B-C(I)								
B-C								
C								
C-D								
D(I)			X	X			X	
D					X		X	X
D-E					X		X	X
E(I)				X				
E	X						X	X
F					X			X
F-G							X	X
G					X		X	X
G-H							X	X
H					X			X
H-I								X
I(I)	X	X	X	X		X	X	X
I					X		X	X
J					X		X	X
J-K					X			X
K(I)	X	X	X	X		X	X	X
K					X	X	X	X
K-L					X	X	X	X
L			X		X	X	X	X
L-M			X			X	X	X
M						X	X	X
M-N						X	X	X
N				X		X	X	X
N-O				X		X	X	X
O	X					X	X	X
O-P	X	X	X	X		X	X	X
P	X	X	X	X		X	X	X

costa the strips overlap each other by 40-50% of their length while in the third transverse costa the overlap is 10-15% (Figs. 6, 7). Since the number of costal strips is constant, this overlap produces transverse costae of different diameters, hence the barrel shape of the lorica. The longitudinal costal strips are blunt at both ends and overlap one another by 10% of their total length (Fig. 7). At or below the posterior transverse costa, a reduction in the numbers of longitudinal costae occurs as they converge and form a caudal appendage (Fig. 8). Mean lorica length (excluding the caudal appendage) and diameter at the third transverse costa were statistically different for stations I and K: $43 \pm 3 \mu\text{m} \times 25 \mu\text{m} \pm 2 \mu\text{m}$ and $33 \pm 6 \mu\text{m} \times 21 \pm 2 \mu\text{m}$, respectively. The presence of a caudal appendage and one

anterior transverse costa with three or four evenly spaced transverse costae posterior to it distinguish *D. multiannulata* from the type species of the genus, *D. grandis* Ellis. *D. multiannulata* differs from *D. pedicellata* Leadbeater by possessing additional transverse costae (*D. pedicellata* has 3) and having anterior projections constructed of more than one costal strip (Fig. 6). The presence of costal strip bundles within loricas was also noted (Fig. 12).

Crinolina aperta (Leadbeater) Thomsen (Figs. 13-16). Loricas of this species were found at most of the southern stations in the ice as well as in the water column (Table 2). The lorica is constructed of twelve longitudinal and two transverse costae with the longitudinal costae continuing beyond both ends of the lorica (Figs. 13, 14).



Figure 6. *Diaphanoeca multiannulata*. Complete lorica with 5 transverse and 11 longitudinal costae. LM. Ice floe pond, station I.



Figure 7. *Diaphanoeca multiannulata*. Whole lorica showing 12 longitudinal and 4 transverse costae, anterior projections, and a caudal appendage. LM. Ice floe pond, station I.

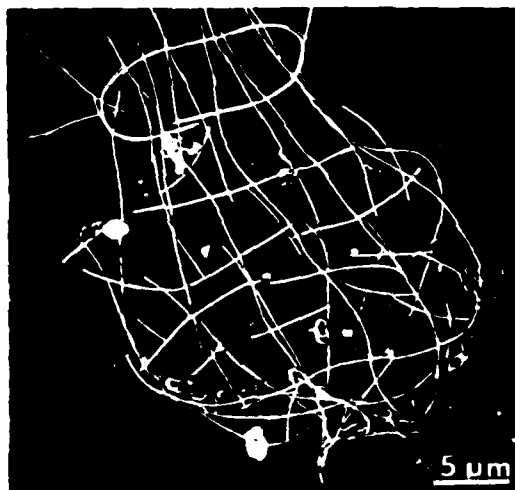


Figure 8. *Diaphanoeca multiannulata*. Whole lorica showing costal strip components of both longitudinal and transverse costae. SEM. Ice floe pond, station I.

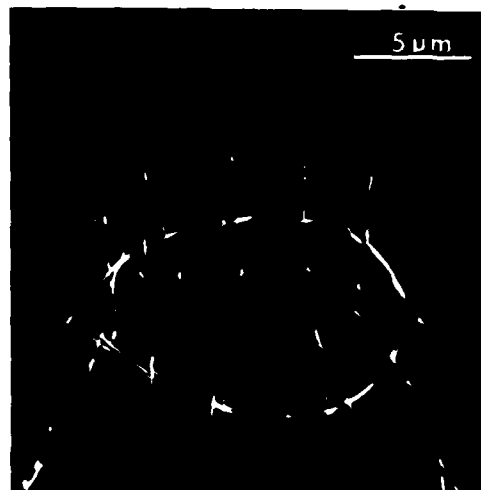


Figure 9. *Diaphanoeca multiannulata*. Anterior transverse costa and anterior projections. Projections are 1/2 costal strips in length. The mode of attachment of the transverse costal strips to each other and to the longitudinal costae is visible. SEM. Ice floe pond, station I.

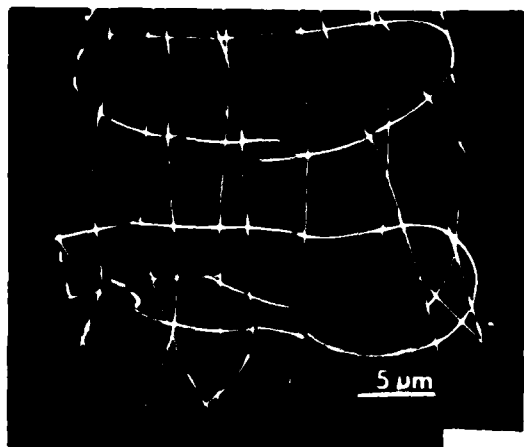


Figure 10. *Diaphanoeca multiannulata*. Partial lorica with intact second and third transverse costae. SEM. Ice floe pond, station I.



Figure 11. *Diaphanoeca multiannulata*. Coalescing of longitudinal costae below the fourth transverse costa. The caudal appendage arises from this stalk. SEM. Ice floe pond, station D.

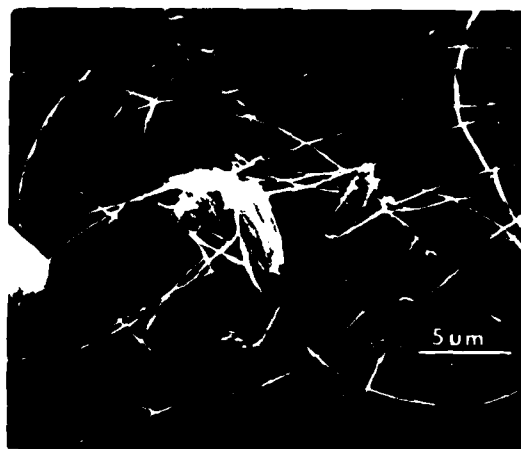


Figure 12. *Diaphanoeca multiannulata*. Incomplete lorica with costal strip bundle. SEM. Ice floe pond, station D.

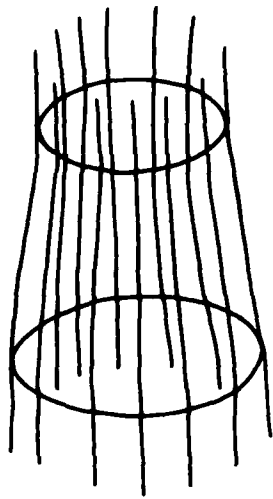


Figure 13. *Crinolina aperta*. Line drawing.



Figure 15. *Crinolina aperta* Lorica showing the size difference between the anterior and posterior transverse costae. LM. Ice floe pond, station L.

The costal strips of the transverse costae are tapered at one end and I-shaped at the other end (Fig. 16). The upturned end of each costal strip on both the transverse costae is directed towards the anterior (narrow) end of the lorica. It is the I-shaped end that is responsible for the at-

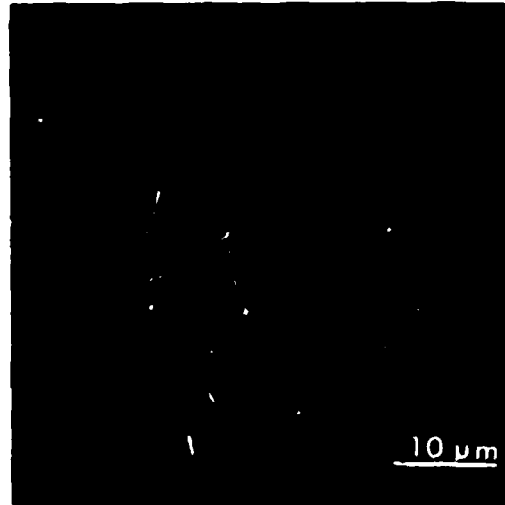


Figure 14. *Crinolina aperta* Lorica with 2 transverse (the smaller of the two is the anterior) costae and 12 longitudinal costae and projections at the posterior and anterior ends. LM. Water column, station L.

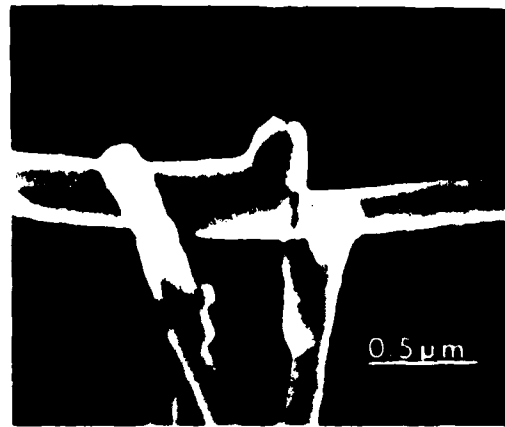


Figure 16. *Crinolina aperta* Section of the anterior transverse costa and a longitudinal costa showing the L-shaped transverse costal strip and the Y-shaped notch made by the longitudinal costa in which the transverse costa sits. SEM. Water column, station L.

tachment of the transverse costa to the longitudinal costae. At the anterior transverse costa the longitudinal costa forms a Y shaped notch in which the transverse costa is situated. The lorica ranged in size from 24–40 μm long, 12–16 μm in diameter at the anterior end and 13–18 μm in

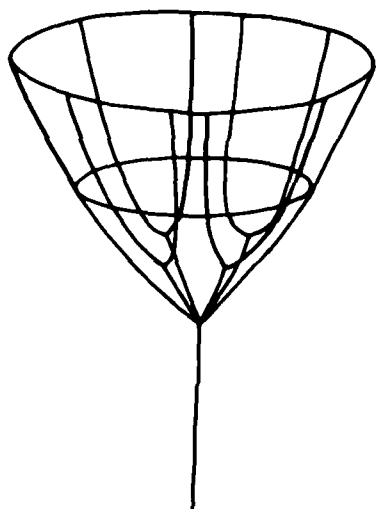


Figure 17. *Parvicorbicula socialis*. Line drawing.

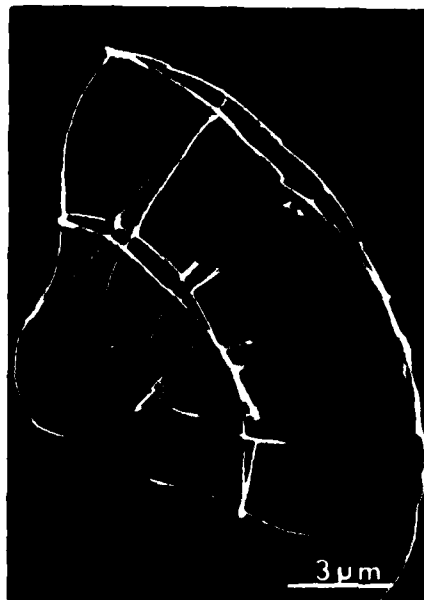


Figure 18. *Parvicorbicula socialis*. Lorica with two transverse and ten longitudinal costae and no caudal appendage. Note the attachment of the distal end of the longitudinal costae to the midpoint of the anterior transverse costal strips. SEM. Water column, station K.

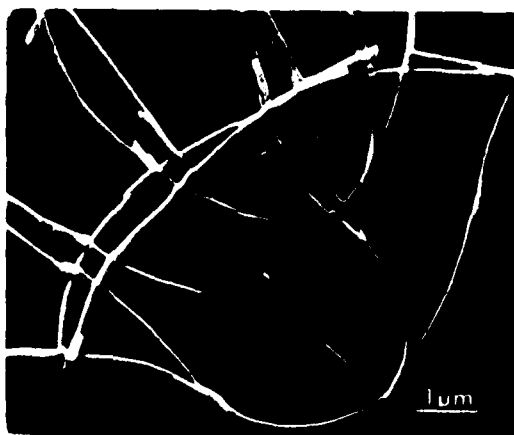


Figure 19. *Parvicorbicula socialis*. Posterior portion of lorica showing the second transverse costa situated at the posterior end of the anterior longitudinal costal strip. Longitudinal costal reduction from ten to five occurs below the second transverse costa before uniting at a point. SEM. Water column, station K.

diameter at the posterior end. Although smaller than those previously reported (Manton et al. 1977) (Appendix A) there is little doubt, based on both gross morphology and costal substructure, that this organism is *C. aperta*.

Parvicorbicula socialis (Meunier) Detlandre (figs. 17-24). This species was encountered at more stations than any other member of the Acanthoecidae, and although it was found in ice samples it seemed to be most abundant in the water column (Table 2). The lorica is composed of ten longitudinal and two transverse costae, possessing in some cases a caudal appendage. The anterior transverse costa is constructed of ten overlapping costal strips, tapered at both ends. The second or posterior transverse costa is constructed of fewer (6 or 7) but similarly shaped costal strips and is situated one costal strip beneath the anterior transverse costa (figs. 18, 19). The longitudinal costae join the anterior transverse costae in the middle of the component costal strips; at the point of contact the



Figure 20. *Parvicorbicula socialis*. Detail of the attachment of the longitudinal costae to the anterior transverse costa showing the enlargement of the anterior end of the longitudinal strips. SEM. Water column station K.



Figure 21. *Parvicorbicula socialis*. Posterior transverse costa showing coalescing of longitudinal costae into a stalk from which a caudal appendage arises. SEM. Water column station K.

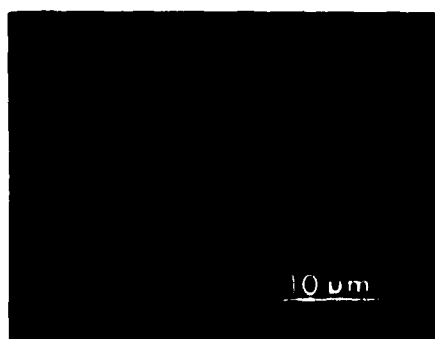


Figure 22. *Parvicorbicula socialis*. Lorica showing longitudinal costal reduction to 1 below the second transverse costa. LM. Water column station I.

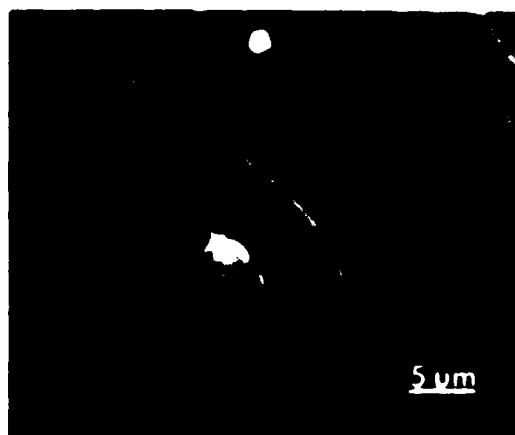


Figure 23. *Parvicorbicula socialis*. Complete lorica with intact cell and flagellum (arrow) projecting out of the anterior end of the lorica. LM. Water column station H1.

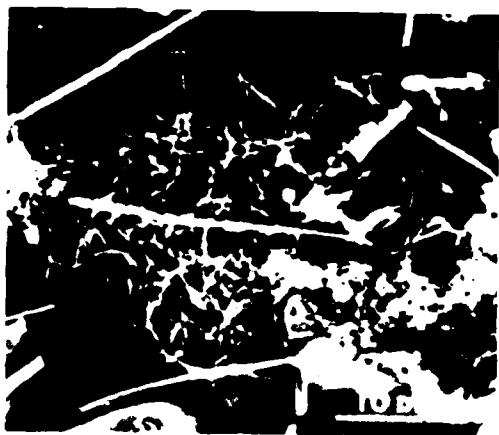


Figure 24. *Parvicorbicula socialis*. Aggregations of loricas, indicating colony formation. LM. Water column, station H-I.

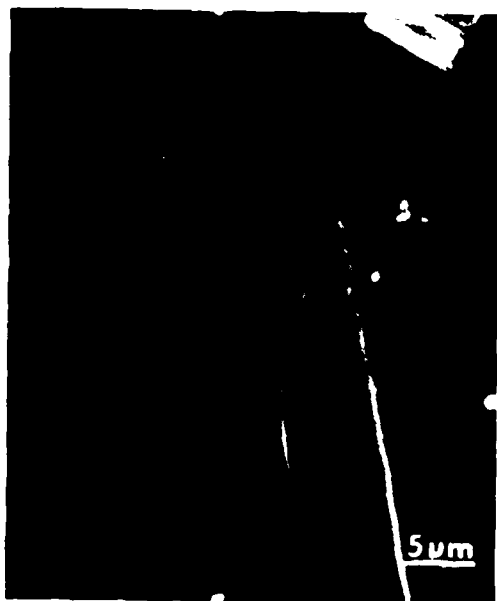


Figure 26. *Acanthoeopsis spiculifera*. Complete loricum with 16 longitudinal and 3 transverse costae, anterior projections and a caudal appendage. LM. Water column, station P.

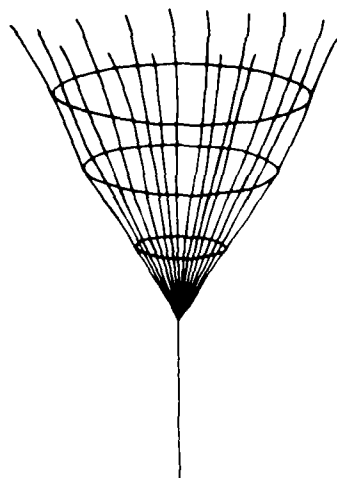


Figure 25. *Acanthoeopsis spiculifera*. Line drawing.

longitudinal costal strip is enlarged (Fig. 20). Reduction in the number of longitudinal costae may occur at or below the second transverse costa (Figs. 18, 19, 21, 22). The longitudinal costae may join together at a point or they may coalesce into a stalk from which a caudal appendage arises (Fig. 21). Both stalked and unstalked loricas were observed. The mean size range of the loricas measured from station I ($n = 10$) was $14 \cdot 12 \mu\text{m}$ (length excluding the caudal appendage + anterior loricum diameter). The protoplast in those loricas where one was observed was situated below the second transverse costa and possessed a flagellum that extended anteriorly out of the loricum (Fig. 23). In several cases aggregations of loricas were observed, indicating colony formation of some sort (Fig. 24).

Acanthoeopsis spiculifera Norris (Figs. 25, 26). This species was found at station P in the water column and in the ice at stations I and K (Table 2). The loricas were approximately $28 \mu\text{m}$ long (excluding caudal appendage) and possessed caudal appendages $11 \mu\text{m}$ long. The loricum was composed of sixteen longitudinal and three

transverse costae (Fig. 26). Projections beyond the anterior transverse costa were observed and the longitudinal costae converged posteriorly to give rise to the caudal appendage. No observations on the subunit structure of the costae was possible due to the scarcity of the organism in this material. There is little doubt that this organism is the species described by Norris (1965) (Appendix A) with the light microscope and examined by Thomsen (1977) with the electron microscope. Discrepancies in lorica size, the number of longitudinal costae, and the arrangement of the transverse costae do exist but it is felt that these differences reflect additional morphological variability not noted by Norris in the Pacific samples with which he worked (Thomsen 1977).

Bicosta spinifera Thomsen (Figs. 27-28). Loricas, both whole and partial, were found at a number of southern stations in the water column and in the ice at four stations (Table 2). The structure of the lorica is simple, lacking transverse costae and possessing but two longitudinal costae (Fig. 28). The longitudinal costae cross each other about two-thirds the length down the lorica and give rise to two sweeping anterior projections and to the caudal appendage posteriorly. The length of the lorica from its base to the top of the anterior projections is 30 μm . The

junction between the longitudinal costae and the anterior projections can be seen as thickening in the costae (see arrow, Fig. 28). The size and gross morphology of the loricas from the Weddell Sea fit well within the original description made with the LM and the subsequent EM study by Reynolds (1976) (Appendix A).

Bicosta antennigera Moestrup (Figs. 29-30). Loricas of this species were observed at stations I and K in the ice and stations O-P and P in the water column (Table 2). The lorica of this species is formed by two short longitudinal costae from which spring the sweeping anterior projections (two) and the caudal appendage. The anterior projections seem to be composed of two costal strips each (Fig. 30) while the caudal appendage and the longitudinal costae appear to be unit structures. The base of the cell is situated at the junction of the longitudinal costae and the anterior projections (Fig. 31). No transverse costae were observed. The total length of the lorica, including the caudal appendage, was 25 μm , the distance between the ends of the anterior projections was also 25 μm . The lorica morphology of the organisms collected from the Weddell Sea agrees well with the type description (Moestrup, 1979) (Appendix A) although they are somewhat smaller in size. Differentiation between *B. minor*

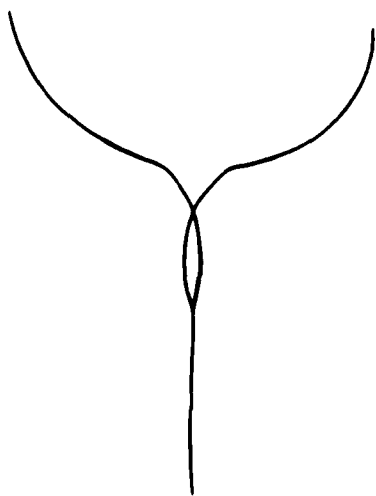


Figure 27. *Bicosta spinifera*. Line drawing

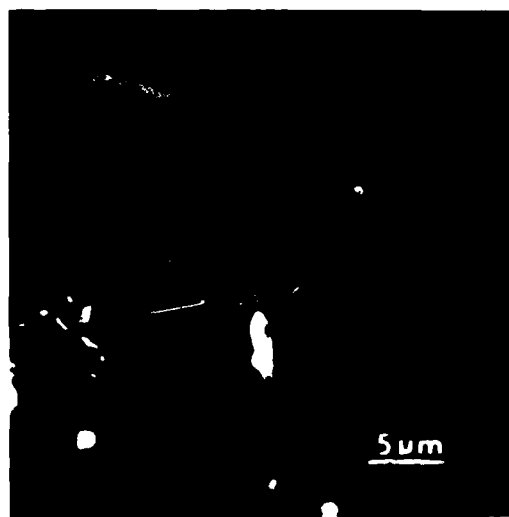


Figure 28. *Bicosta spinifera*. Lorica with 2 longitudinal and no transverse costae and a caudal appendage. The junction of the anterior projection and the longitudinal costa is denoted by a thickening (arrow). LM. Water column, station L-M.

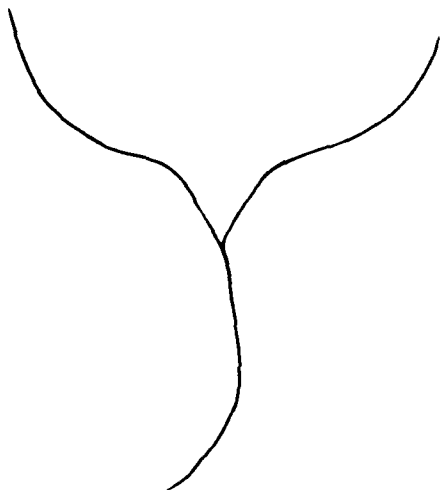


Figure 29. *Bicosta antennigera*. Line drawing.

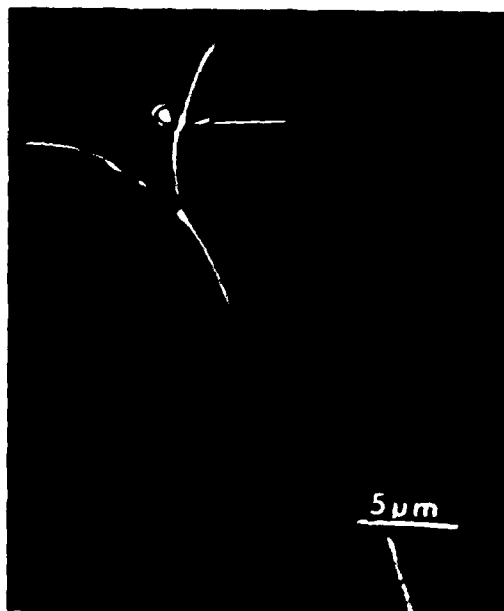


Figure 31. *Bicosta antennigera*. Complete lorica with cell, 2 longitudinal and no transverse costae, anterior projections and a caudal appendage. LM. Ice floe pond, station 1.

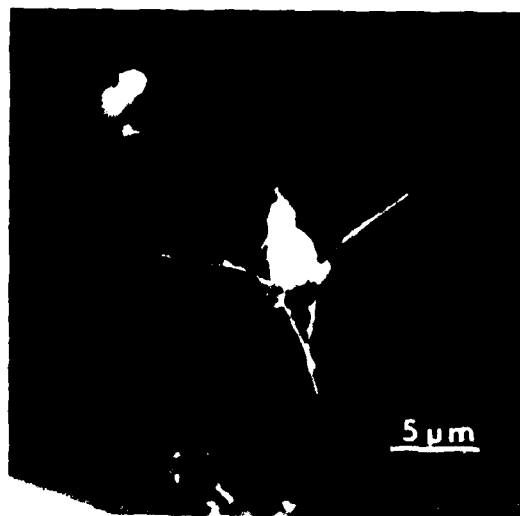


Figure 30. *Bicosta antennigera*. Lorica lacking the distal ends of the anterior projections. Note junctions of the anterior projection and the longitudinal costa (arrow). LM. Water column, station O-P.

(Reynolds) Leadbeater and this species found in the Antarctic involves the number of costal strips which make up the lorica chamber (two for *B. antennigera* vs. four for *B. minor*) as well as the orientation of the lorica chamber and the anterior projections.

Calliacantha simplex Manton and Oates (Figs 32-34). Specimens in various conditions were obtained from both the water column and ice at a number of stations (Table 2). Lorica construction consists of two transverse and four longitudinal costae, anterior projections and a caudal appendage. The second transverse costa is made up of costal strips with a smaller diameter than those of the other costae and is situated about one fourth the length of the lorica below the anterior transverse costa (Figs 33, 34). The anterior transverse costa is angular in shape (Fig. 34) and is apparently formed from just four costal strips. The lorica (excluding the caudal appendage) is 10-14 μm long and has a diameter of approximately 11 μm at the anterior transverse costa. The caudal appendage is 7 μm long while the anterior projections are 14 μm long. These dimensions agree quite well with those given in the type description (Appendix A) (Manton and Oates 1979b). The revised taxonomic description

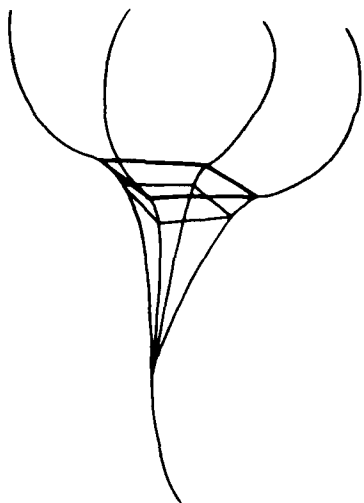


Figure 32. *Calliacantha simplex*. Line drawing.

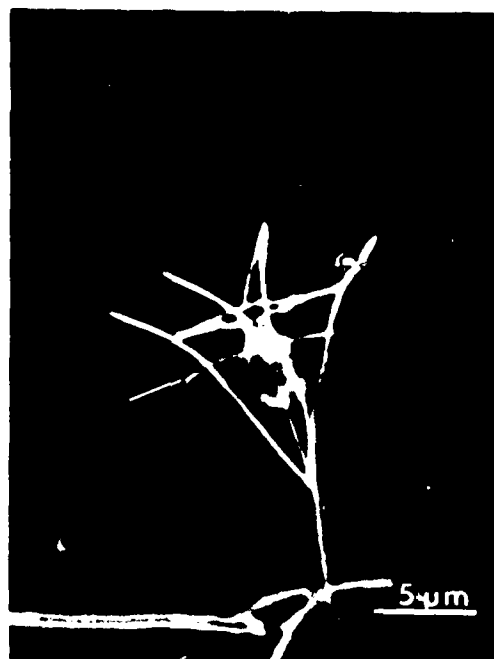


Figure 33. *Calliacantha simplex*. Lorica with 2 transverse (arrow denotes position of the second transverse costa) and 4 longitudinal costae, incomplete anterior projections and a caudal appendage. LM. Ice floe pond, station 1.

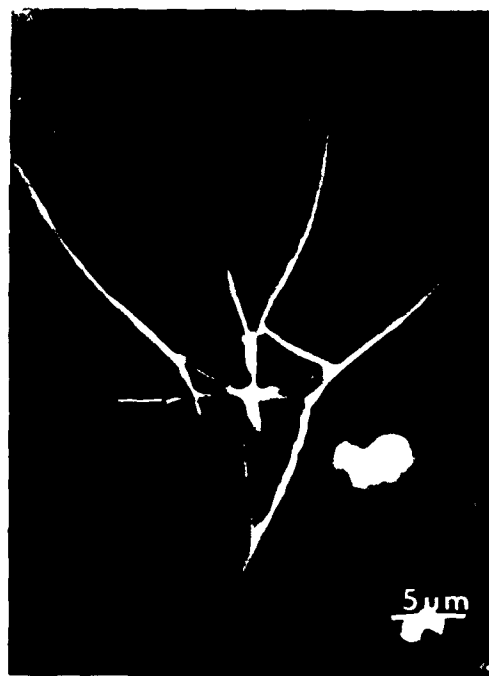


Figure 34. *Calliacantha simplex*. Lorica with 2 transverse (arrow denotes the position of the second transverse costa) and 4 longitudinal costae, complete anterior projections, and an incomplete caudal appendage. LM. Ice floe pond, station 1.

of *C. natans* (Grøntved) Leadbeater, the type species of the genus, defines *C. natans* as having three anterior projections and six longitudinal costae with the anterior projections arising independently of the longitudinal costae (Manton and Leadbeater 1978). The light micrographs of the present study as well as the electron micrographs of the type description show that *C. simplex* possesses four longitudinal costae and an equal number of anterior projections which are continuous with the longitudinal costae (Manton and Oates 1979a).

Calliacantha multispina Manton and Oates (Figs. 35-38). Organisms of this designation were found in four of the five ice samples and at the four southern stations (Table 2). The shape of the lorica (conical), the presence of both anterior projections and a caudal appendage, and the number of longitudinal (six) and transverse (two) costae present characterize this organism and

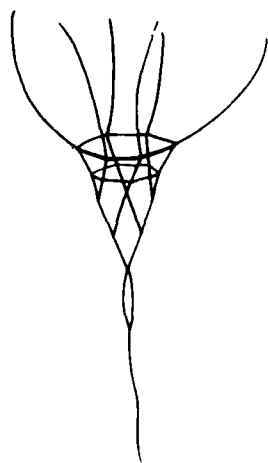


Figure 35. *Calliacantha multispina* aff. Line drawing.



Figure 37. *Calliacantha multispina* aff. Incomplete lorica showing 5 longitudinal and 2 transverse costae. The anterior transverse costa is thicker than the second transverse costa. Note the twist in the longitudinal costae (arrow) and the simultaneous longitudinal costal reduction (arrow). LM. Water column, station O-P.



Figure 36. *Calliacantha multispina* aff. Orientation of the lorica showing the full extent of the caudal appendage and anterior projections. Note twist in the longitudinal costae (arrow) and the simultaneous longitudinal costal reductions (arrow). LM. Water column, station O-P.

place it within the genus *Calliacantha*. The longitudinal costae undergo two reductions (see arrows, Figure 36-38) as they posteriorly converge. After the second reduction the longitudinal costae appear to cross and possibly fuse (Figures 36-38). The caudal appendage arises from the convergence of the longitudinal costae. The reduction in numbers of longitudinal costae occurs simultaneously on each side of the lorica with respect to the distance from the base of the lorica. The costal strips of the anterior transverse costa are thicker than those of the second transverse costa or longitudinal costae. The second transverse costa is situated approximately one fifth the total length of the lorica below the anterior transverse costa. The length of the lorica (excluding the caudal appendage) is 26 μm , the diameter at the anterior transverse costa is 9 μm and the caudal appendage is 15 μm long. These dimensions are within the range given for the type description (Appendix A) (Manton and Oates 1979a, Manton and Oates 1979b) with an "unusual duplication" (presumably the twist) at



Figure 38. *Calliacantha multispinosa* aff. *Incomplete lorica* showing 2 transverse and 5 longitudinal costae and 6 anterior projections. Note the longitudinal twist (arrow) and the simultaneous costal reductions (arrow). LM. Ice floe pond, station E.

the posterior end (Manton, pers. comm.). The description of the type of the genus, *C. natans*, allows for the reduction of the six longitudinal costae to as few as three before coalescence at the posterior end. If it were not for this discrepancy and the posterior twist, the organisms in Figures 36-38 would be very similar to *C. natans*. Until further observations can be made, the organisms in Figures 36-38 will be designated *C. multispinosa* aff.

The key in Table 3 was prepared to assist in identifying the loricas of the species of Acanthoecidae found in samples from the Weddell Sea.

Distribution and environmental tolerances

The distribution of loricate choanoflagellates in the Weddell Sea is summarized in Table 2 by station; Table 1 presents pertinent geographical,

sampling, and environmental data. General trends in the distribution include an increase in diversity (as measured by the numbers of species present) from the northern stations to the southern stations and the presence of a few species, notably *P. socialis* and *D. multiannulata*, at most or all of the stations where choanoflagellates were recorded. As mentioned in the observations, some species, *A. spiculitera* and *B. antennigera*, were absent from all but a few stations. Ice stations I and K had not only more species than the matching water column stations but more than any other stations sampled.

Temperatures and salinities for the water column at the stations where these measurements were taken (Table 1) can be approximated by the surface temperatures and salinities due to the well mixed nature of the upper water column from which the samples were taken (El-Sayed and Taguchi 1979). The temperature range of -2.4° to 1.7°C represents a maximum difference of 4.1°C while the salinity range of $33.2^{\text{‰}}$ to $34.3^{\text{‰}}$ represents a maximum difference of $1.1^{\text{‰}}$. The relative uniformity of the two environmental parameters studied prevents explanation of the distribution of loricate choanoflagellates from the water column based upon salinity and temperature alone.

Measurements of salinity and temperature of the ice floe ponds were not obtained in the field. The temperature can be approximated to be between the air temperature (about 0°C) and the water temperature, placing it within the range of temperatures observed at the surface of the water column. Ponds that form on sea ice can do so in two different ways, either through solar induced melting or subsidence of the floe and subsequent flooding. In the case of the ponds encountered in the Weddell Sea there is strong evidence to suggest the latter case. All the ponds encountered were near deformational features such as ridges where the topside loading would deflect the flat plate floe so that the surface would be below sea level, allowing it to be flooded through cracks or connections to the open water (S. Ackley, pers. comm.). Therefore the salinity of the ponds should approximate that of sea water or be somewhat less if snow was incorporated into the water of the pond. The ice core sample was not accompanied by temperature observations, although the assumption that the temperature, particularly of the brine pockets and fissures, must be at or below freezing (-1.8°C for sea water at $36^{\text{‰}}$) would seem to be valid. Salinities of 10-cm sections of the core

Table 3. Key for the identification of loricas of Acanthoecidae from the Weddell Sea.

A	Lorica possessing projections of the longitudinal costae beyond the transverse costa (e) at one or both ends (If yes then B)	
AA	Lorica not possessing projections of longitudinal costae beyond the transverse costa (e)	<i>Parvicorbicula socialis</i>
B	Longitudinal projections of costae present only at anterior end of lorica, posterior end characterized by a coalescence of the longitudinal costae and a caudal appendage (If yes then C)	
BB	Longitudinal projections of costae present at both ends of lorica	<i>Crinolina aperta</i>
C	Lorica composed of 6 or fewer longitudinal costae and 2 or fewer transverse costae (If yes then 1)	
CC	Lorica composed of 10 or more longitudinal costae and 3 or more transverse costae (If yes then D)	
1	Lorica composed solely of 2 longitudinal costae (If yes then A)	
1'	Lorica composed of four to six longitudinal and two transverse costae (If yes then 2)	
a	Longitudinal costae spiraled or twisted about one another	<i>Bicosta spinifera</i>
aa	Longitudinal costae not spiraled or twisted about one another	<i>Bicosta antennigera</i>
2	Anterior projections 4, continuous with longitudinal costae	<i>Calliacantha simplex</i>
2'	Anterior projections 6, continuous with longitudinal costae	<i>Calliacantha multispina</i>
D	Longitudinal costae 14 or more, transverse costae 3, largest diameter of the lorica at the anterior transverse costa	<i>Acanthoecopsis spiculifera</i>
DD	Longitudinal costae 13 or fewer, transverse costae 4 or more, largest diameter of lorica at third or fourth transverse costa	<i>Diaphanoeca multiannulata</i>

were determined, and showed a maximum of 6‰ at a depth of 120-130 cm below the surface (ice floe thickness was 145 cm) (Ackley et al 1979). This, however, does not represent the salinity of the brine pockets and fissures where it is hypothesized that the choanoflagellates exist. In the brine pockets and fissures, salinity varies due to the variable degree of freezing throughout the floe. In some of the smaller pockets (where the greatest amount of freezing and brine were found) salinity exceeds that of the water from which the ice was formed.

DISCUSSION

Morphology

The use of SEM as a tool in the morphological and taxonomic aspects of this study has revealed that the manner in which transverse costae within an organism vary their diameters is a character that is probably important in the establishment of a species concept for the Acanthoecidae. The variation of the transverse costae ultimately determines lorica shape, a widespread characteristic used in describing genera. In *Parvicorbicula socialis*, *P. quadricostata* Thronsen, and *P. circularis* Thomsen, the

characteristic cone shape of the genus is achieved by having a posterior transverse costa (there are but two transverse costae) of smaller diameter than the anterior transverse costa (Manton et al 1976, Thomsen 1976). The number of component costal strips is less in the posterior than the anterior transverse costa, while the length and degree of costal strip overlap is approximately equal. In *Pleurasiga reynoldsii* Thronsen, a barrel shape is achieved by having an anterior transverse costa with a larger diameter than the posterior transverse costa (this species also has only two transverse costae). This variation in costal diameter is achieved by having anterior costal strips of greater length than those of the posterior transverse costa. The numbers and degree of the costal strip overlap are constant (Thomsen 1976). In *Crinolina isetiordensis*, the skirt-shaped lorica is achieved by having two transverse costae of different diameters. In this case, however, a combination of costal strip length and degree of overlap is used to achieve this effect (Thomsen 1976). In *Diaphanoeca pedicellata* Thronsen, a barrel-shaped lorica is achieved by having two transverse costae with the same number of transverse costal strips but with a lesser degree of overlap in the second transverse costa. Transverse costal strip length is

constant (Thomsen 1976). *D. multiannulata* shares this method of lorica shape control although it is somewhat more elaborate because four costae are involved. The exactness of deposition of component costal strips is indicated by the differences in size and morphology not only between transverse and longitudinal costae but between individual transverse costae in some cases (*Calliacantha simplex*). The differences in the manner of lorica shape determination between the genera (investigated to date by electron microscopy) and the exactness of costal strip deposition indicate that this character may be potentially important from a taxonomic standpoint, both in assigning new species to a genus or in reassigning species described without attention to this detail. More investigations with the electron microscope will be needed before the taxonomic potential of this character can be fully appreciated, but the results of this study indicate that the manner in which the lorica shape is determined may be a conservative characteristic.

Another morphological consideration that deserves further investigation with respect to its contribution to the taxonomy and phylogeny of this group is the size range of a species. The difficulty of determining diameters and lengths of two-dimensional representations of three-dimensional structures notwithstanding, the size of the loricas of a species seems to have an inverse relationship with the temperature of the environment in which they are found (Manton et al. 1976, Manton and Leadbeater 1978). This is borne out in the present study to some extent. *A. spiculifera*, which has a temperate type locality, was considerably larger than the type specimen; however, *B. spinifera* and *C. aperta* were considerably smaller than the type specimen. The discrepancies between the size ranges of the two bipolar species are difficult to comprehend. Seasonal (winter-summer) forms of *Parvicorbicula socialis* with distinct and different size ranges have been observed in the Arctic (Manton et al. 1976), and it is possible that this sort of phenomenon is responsible for the discrepancies noted here. It is suggested that lorica size, although an easily discernible characteristic with the light microscope, not be utilized to differentiate species, at least until a more comprehensive picture emerges.

Distribution

The reports of *B. spinifera*, *C. aperta*, *A. spiculifera*, and *C. simplex* from the Weddell Sea repre-

sent a significant extension of the geographical range of the four species. *B. spinifera* has been reported from its type locality, the Norwegian Arctic (Thronsdon 1970a), from fjords of Norway (Leadbeater 1972a), and from fjords of Denmark (Thomsen 1973). *C. aperta* has been reported only from its type locality at Cornwallis Island in the Canadian Arctic (Manton et al. 1975). *A. spiculifera* has been reported from its type locality on the Washington coast (Norris 1965) and from the coast of Finland (Thomsen 1977). *P. socialis* has been reported from Terre Adelie (Detlandre 1960) in the Antarctic as well as from many other localities throughout the world (Manton et al. 1976). This and other studies indicate that choanoflagellates prefer temperate and polar regions although subtropical and tropical regions need to be investigated before this can be confirmed.

The spatial distribution of choanoflagellates within the Weddell Sea over a cruise track that covered approximately 1000 nautical miles indicates that loricate choanoflagellates were generally present, although in small quantities for some species, at the time of sampling (Table 2). The paucity of some organisms may indicate the true population, may mirror equipment selectivity whereby some of the smaller organisms slip through, or may be caused by the destruction of the less robust forms as a result of the preservation and preparation techniques. Additional studies on the spatial and temporal distribution (keeping in mind the effects of collection, preservation, and preparation techniques) of choanoflagellates need to be carried out before a complete picture of the biogeography will begin to emerge. The presence of choanoflagellates over a vast, albeit relatively uniform, area indicates that many of these organisms may be cosmopolitan, certainly *P. socialis* is ubiquitous. However, there is a paucity of reports in which choanoflagellates are present as part of the fauna. Special sampling techniques and an awareness on the part of researchers of the existence of choanoflagellates would lead to their inclusion in future studies.

Habitat

The association of choanoflagellates possessing caudal appendages and anterior projections with the sea ice has been suggested by Manton et al. (1975). It is tempting to arrive at the same conclusion for the Weddell Sea when it is noted that six of the seven species reported from this

area possess these appendages. If this conclusion is valid, then the presence of choanoflagellates in the water column could be the result of seeding from the ice. Breakup of sea ice along the open ocean/pack ice interface does occur and is responsible for the release of dense algal populations into the water column (Ackley et al. 1979). Presumably this seeding could be a method of introducing choanoflagellates from the sea ice into the water column. Quantitative studies of ice algae and water column algae from the same areas indicate that there are species which not only prefer the ice environment, but even flourish in it (Ackley et al. 1978). No comparable quantitative studies were done with choanoflagellates, largely because accurate methods for enumeration have not been developed. This limits the extent of our ability to define preferred habitats or conclude whether the Acanthoecidae observed in the water column are autochthonous or were introduced from the ice. Choanoflagellates in this study are definitely ice-dwellers, as there is no other mechanism to allow for their transport from the water to the ice (with the exception of initial freezing). Quantitative studies of samples obtained from transects perpendicular to the ice edge would establish whether the choanoflagellates found in the water column were native or not.

Ice is an ecologically interesting habitat for choanoflagellates for several reasons. The disadvantages usually associated with an ice environment include freezing or subfreezing temperatures and osmotic and metabolic stresses not normally encountered in the open ocean. The temperature in the ice during the austral winter, a period of time during which choanoflagellates have to survive if not grow, can be calculated by assuming a linear change between the water underlying the ice (about -1.8°C) and the air temperature, which during the winter is well below freezing. Assuming that the ice was 2 m thick, water temperature was -1.7°C , air temperature was -20°C , and the heat conductivity of ice is constant, then the temperature and salinity 30 cm from the bottom of the ice floe are -4.45°C and 44.7‰ (Meguro et al. 1967). The mechanism with which the choanoflagellates, and ice algae for that matter, cope with these low temperatures and osmotic stresses remains unknown. However, tide pool organisms, including those choanoflagellates recorded by Norris (1965), must cope with greater extremes in salinity and temperature mediated by periods of

evaporation and precipitation. All evidence from field studies indicates that, as a group, choanoflagellates have great environmental tolerances. Work with organisms in culture could confirm not only general patterns but also tolerance levels for individual species.

On the other hand the advantages of inhabiting the ice are twofold. The ice provides a spatially stable environment like that in which choanoflagellates have been found most often and presumably prefer and in which food is thought to be abundant. The ice community, predominantly pennate diatoms, choanoflagellates, and bacteria, is trapped within the ice until, in the case of the Weddell Sea community, physical or mechanical breakup wrought by the winds, waves, and tides releases them. Not only does the ice provide a substrate in which the choanoflagellates can grow but the algal standing crop is conserved within the ice (until such release occurs, predominantly along the ice edge) resulting in high standing crops of algae (maximum chlorophyll a values ranged from 0.3 to 4.4 mg/m^2 for those cores examined) (Ackley et al. 1978). Although little or no work has been done on bacterial populations within the ice, given the high concentrations of algae and the resultant dissolved organic matter, it would seem safe to assume that they are high. Choanoflagellates feed on bacteria (Leadbeater and Morton 1974a, Ellis 1930) and may be able to use the dissolved organic matter directly (Gold et al. 1970). Sieburth et al. (1978) place choanoflagellates in the ecological category of protozooplankton, a group defined as being unicellular and possessing a size, metabolic activity, and division rate similar to phytoplankton although they are included in the animal kingdom. Protozooplankton are considered beneficial to the phytoplankton because they recycle the nutrients stored in the bacteria, which live off the dissolved organic matter and dead cells of the algae. Choanoflagellates provide for a rapid conversion of bacterial biomass to nutrients. A tightly coupled trophic scheme exists in the interstitial pockets of brine within the ice, at least until release to the ocean occurs. A more classical trophic scheme between bacteria and larger metazooplankton is postulated for the choanoflagellates in the water column. It appears that the disadvantages of being associated with an environment with extremes of temperature and salinity are outweighed by the presence of a substrate, lack of predators, and the availability of food sources. This ice system with

its three main components deserves more attention than it has hitherto received, keeping in mind the elucidation of above-mentioned relationships and their quantitation.

SUMMARY

Conclusions

1. Choanoflagellates were widely distributed throughout the region of the sea ice edge in the Weddell Sea. Eight species, including one described for the first time, were observed in water column and ice floe samples.

2. The tolerance of the low temperatures and high salinities, characteristic of the Weddell Sea ice community, by all eight species has been established.

3. The geographical range of five species of Acanthoeidae (*Crinolina aperta*, *Parvicorbicula socialis*, *Bicosta spinifera*, *Bicosta antennigera*, and *Acanthoeopsis spiculifera*) has been significantly expanded.

4. The mechanism of shape control of the lorica may be conservative and potentially useful as a taxonomic character.

5. The size of loricas is judged not to be a good taxonomic character because of the variability within species reported from different areas of the world.

Recommendations for future work

It may be concluded from compilation of evidence from the present work and other studies that choanoflagellates of the Family Acanthoeidae are, in general, cosmopolitan, euryhaline and eurythermal, and dwell in many marine habitats. Biogeography, spatial distribution, environmental tolerances, associations with the ice community, morphology, and taxonomy of the Acanthoeidae, all addressed to some extent in this report, need further investigation. Development of a method for enumeration, an increased awareness on the part of researchers of the presence of choanoflagellates, and widespread sampling in all geographic regions and seasons would advance our understanding of the biogeographical distribution of this group. A more comprehensive examination of the components of the ice community with the goal of understanding its trophodynamics is needed.

All future studies must be based upon a firm taxonomic background that is itself based on

morphological and phyletic relationships. Although the advent of electron microscopy has greatly expanded the morphological base by increasing resolution, depth of field, and the ability to discern surface detail, it is hoped that more emphasis on conservative features such as costal strip shape, relative size of the costal strips, and methods of control of lorica shape will play greater roles in establishing this morphological base. However, the need for light microscopy to identify and enumerate field samples should not be forgotten.

LITERATURE CITED

- Ackley, S. F., S. Taguchi and K. Buck (1978) Primary productivity in sea ice of the Weddell region. U.S. Army Cold Regions Research and Engineering Laboratory, CRRRI Report 78-19, 17 p.
- Ackley, S. F., K. R. Buck and S. Taguchi (1979) Algal standing crop of the sea ice of the Weddell region. *Deep Sea Research*, vol. IV, no. 26A, p. 269-281.
- Detlandre, G. (1960) Sur la presence de *Parvicorbicula socialis* (Meunier) dans le plancton de l'Antarctique (Terre Adélie). *Revue algologique N.S.*, vol. 5, p. 183-185.
- Ellis, W. N. (1930) Recent researches on the Choanoflagellata (Craspedomonadines) (freshwater and marine). *Annales de la Société Zoologique de Belgique*, vol. 60, p. 49-88.
- El-Sayed, S. Z. and S. Taguchi (1977) Phytoplankton studies in the water column and pack ice of the Weddell Sea. *Antarctic Journal of the U.S.*, vol. 12, p. 35-36.
- Eryxell, G. A. and G. R. Hasle (1970) Diatoms: cleaning and mounting for light and electron microscopy. *Transactions of the American Microscopical Society*, vol. 89, p. 469-474.
- Gold, K., R. M. Pfister and V. R. Uquori (1970) Axenic cultivation and electron microscopy of two species of choanoflagellates. *Journal of Protozoology*, vol. 17, p. 210-212.
- Hibberd, D. I. (1975) Observations on the ultrastructure of the choanoflagellate *Codosiga botrytis* (Ehr.) Saville-Kent with special reference to the flagellar structure. *Journal of Cell Science*, vol. 17, p. 191-219.
- Hibberd, D. I. (1976) The ultrastructure and taxonomy of the Chrysophyceae and Prymnesiophyceae (Haptophyceae). A survey with some new observations on the ultrastructure of the Chrysophyceae. *Botanical Journal of the Linnean Society*, vol. 72, p. 55-80.
- Leadbeater, B. S. C. (1972a) Fine structural observations on some marine choanoflagellates from the coast of Norway. *Journal of the Marine Biological Association of the United Kingdom*, vol. 52, p. 67-79.
- Leadbeater, B. S. C. (1972b) Ultrastructural observations on some marine choanoflagellates from the coast of Denmark. *British Phycological Journal*, vol. 7, p. 195-211.
- Leadbeater, B. S. C. (1973) External morphology of some marine choanoflagellates from the coast of Yugoslavia. *Archiv für Protistenkunde*, vol. 115, p. 234-252.
- Leadbeater, B. S. C. (1975) A microscopical study of the marine

- choanoflagellate *Savillea micropora* (Norris) comb. nov., and preliminary observations on lorica development in *S. micropora* and *Stephanoeca diplocostata* Ellis. *Protoplasma*, vol. 83, p. 111-129.
- Leadbeater, B. S. C. (1977) Observations on the life history and ultrastructure of the marine choanoflagellate *Choanoecca perplexa* Ellis. *Journal of the Marine Biological Association of the United Kingdom*, vol. 57, p. 285-301.
- Leadbeater, B. S. C. (1978) *Renaming of Salpingoeca sensu Grøntved*. *Journal of the Marine Biological Association of the United Kingdom*, vol. 58, p. 511-515.
- Leadbeater, B. S. C. and I. Manton (1974) Preliminary observations on the chemistry and biology of the lorica in a collared flagellate (*Stephanoeca diplocostata* Ellis). *Journal of the Marine Biological Association of the United Kingdom*, vol. 54, p. 269-276.
- Leadbeater, B. S. C. and C. Morton (1974a) A light and electron microscope study of the choanoflagellates *Acanthoecca spectabilis* Ellis and *A. brevipoda* Ellis. *Archiv für Mikrobiologie*, vol. 95, p. 279-292.
- Leadbeater, B. S. C. and C. Morton (1974b) A microscopical study of a marine species of *Codosiga* James-Clark (choanoflagellata) with special reference to the ingestion of bacteria. *Biological Journal of the Linnean Society*, vol. 6, p. 337-347.
- Manton, I. and B. S. C. Leadbeater (1978) Some critical qualitative details of lorica construction in the type species of *Calliacantha* Leadbeater (choanoflagellata). *Proceedings of the Royal Society of London B*, vol. 203, p. 49-57.
- Manton, I. and K. Oates (1979a) Further observations on Choanoflagellates in the genus *Calliacantha* Leadbeater with special reference to *C. multispina* sp. nov. from South Africa and Britain. *Journal of the Marine Biological Association of the United Kingdom*, vol. 59, p. 207-13.
- Manton, I. and K. Oates (1979b) Further observations on *Calliacantha* Leadbeater (choanoflagellata) with special reference to *C. simplex* from many parts of the world. *Proceedings of the Royal Society of London B*, vol. 204, p. 287-300.
- Manton, I., J. Sutherland and B. S. C. Leadbeater (1975) Four new species of choanoflagellates from arctic Canada. *Proceedings of the Royal Society of London B*, vol. 189, p. 15-27.
- Manton, I., J. Sutherland and B. S. C. Leadbeater (1976) Further observations on the fine structure of marine collared flagellates (choanoflagellata) from arctic Canada and west Greenland: species of *Parvicorbicula* and *Pleurisiga*. *Canadian Journal of Botany*, vol. 54, p. 1942-1955.
- Meguro, H., K. Ito and H. Fukushima (1967) Bottom type plankton (ice) in the Arctic Ocean. *Antarctic Record*, vol. 28, p. 2257-2271.
- Moestrup, A. (1979) Identification by electron microscopy of marine nanoplankton from New Zealand including the description of four new species. *New Zealand Journal of Botany*, vol. 17, p. 61-95.
- Norris, R. E. (1965) Neustonic marine Craspedomonadales (choanoflagellates) from Washington and California. *Journal of Protozoology*, vol. 12, p. 589-602.
- Reynolds, N. (1976) Observations on *Salpingoeca spinifera* Thronsdalen and *S. minor* sp. nov. (Craspedophyceae). *British Phycological Journal*, vol. 11, p. 13-17.
- Sieburth, J. McN., V. Smetacek and J. Tenz (1978) Pelagic ecosystem structure: heterotrophic compartments of the plankton and their relationship to plankton size fractions. *Limnology and Oceanography*, vol. 23, p. 1256-1264.
- Thomsen, H. A. (1973) Studies on marine choanoflagellates I. Silicified choanoflagellates of the Isetjord (Denmark). *Ophelia*, vol. 12, p. 1-26.
- Thomsen, H. A. (1976) Studies on marine choanoflagellates II. Fine structural observations on some silicified choanoflagellates from Isetjord (Denmark), including the description of two new species. *Norwegian Journal of Botany*, vol. 23, p. 33-51.
- Thomsen, H. A. (1977) Studies on marine choanoflagellates III. An electron microscopical survey of the genus *Acanthoeccopsis*. *Archiv für Protistenkunde*, vol. 119, p. 86-99.
- Thronsdalen, J. (1969) Flagellates of Norwegian coastal waters. *Nytt magasin for botanikk*, vol. 16, p. 161-216.
- Thronsdalen, J. (1970a) *Salpingoeca spinifera* sp. nov., a new planktonic species of the Craspedophyceae recorded in the Arctic. *British Phycological Journal*, vol. 5, p. 87-89.
- Thronsdalen, J. (1970b) Marine planktonic Acanthoeccaceans (Craspedophyceae) from arctic waters. *Nytt Magasin for Botanikk*, vol. 17, p. 103-111.
- Thronsdalen, J. (1974) Planktonic choanoflagellates from North Atlantic waters. *Sarsia*, vol. 56, p. 95-122.

APPENDIX A. TYPE DESCRIPTIONS OF ACANTHOECIDAE COLLECTED FROM THE WEDDELL SEA.

Crinolina aperta

Original description: Leadbeater, 1975

Lorica barrel-shaped, open at both ends, with a long fringe of slender projecting costae around each opening. Overall length 45-50 μm , width at the anterior end 17-25 μm , at the posterior end 25-35 μm . Number of longitudinal costae 12, each composed of 9 or 10 costal strips with overlapping ends and with a firmly constructed costa located at a distance of 2 costal strips from the anterior end of the lorica, and another located 3 or 4 costal strips from the posterior end. Transverse costal strips L-shaped, tapered at one end and sharply upturned at the other, those from the anterior ring thicker than those from the posterior ring but both thicker than the longitudinal costae; all upturned tips in both transverse costae directed towards the anterior end of the lorica and each individually attached to the corresponding longitudinal costa. Protoplast located centrally ca. 8 μm long \times 5 μm wide, with a flagellum ca. 40 μm long and a ring of about 50 tentacles, each up to 8 μm long. Type locality: Resolute Bay, Cornwallis Island (lat. 74°40'N, long. 95°00'W).

Acanthoecopsis spiculifera

Original description: Norris, 1965

Cells with a form typical for choanoflagellates. Cell enclosed by a lorica composed primarily of 14 longitudinal costae, closely enveloping cell body, spreading slightly at collar to form a broad chamber enclosed by widely spaced costae. Tips of costae free from one another, two or three transverse costae encircling the longitudinal costae at the point occupied by cell's anterior end; two or three other transverse costae encircling lorica just above cell base. Base of lorica attenuate, longitudinal costae converging to form a stalk up to 56 μm long. Lorica 15-18 μm long, lorica body 8-9 μm long, lorica neck (spines) 8-10 μm long, neck dia. up to 10 μm , cell dia. 4-5 μm . Dia. of stalk approximately 0.3 μm .

Type locality: Tide pool at Turn Is., San Juan County, Wash.

Bicosta spinifera

Original description: Throndsen, 1970a

Cell solitary, collarless, egg shaped to cylindrically ovoid, with single collar, flagellum single, about 4 times the length of the cell, nucleus anterior; lorica extremely hyaline, more or less goblet-shaped with 2 (occasionally 3) obliquely running longitudinal ridges winding slightly spirally on the outer surface and continuing apically as slender curved spines, posteriorly merging to make a long posterior projection; cell length: 6-9 μm ; diameter: 3-4 μm , lorica length with anterior and posterior projections: 50-80 μm . Habitat: the sea in the vicinity of Bear Island, 74°30'N, 25°E (1-5°C).

Bicosta antennigera

Original description: Moestrup, 1979

Solitary, protoplast c. 6 μm long, with a single anterior flagellum, 16-18 μm long. The cell located in a lorica composed of seven costal strips. Two costal strips, each 8-10 μm long, form the lorica chamber which contains the protoplast. Anteriorly each of the strips joins with a long anterior spine, 32-37 μm long and made of two costal strips. These differ in length, the proximal being 8-10 μm long, the distal, which is tapering and curves inwards, measures 23-28 μm . Posteriorly the strips of the lorica chamber overlap and join with a posterior spine, c. 25 μm long, made of a single costal strip. Total length of the lorica c. 60 μm .

Type micrograph: Figure 41 from Kaikoura, New Zealand (42°25'S, 173°42'E) 13 September 1974

Calliacantha simplex

Original description: Manton and Oates, 1979b

Lorica with four anterior spines, each continuous with a longitudinal costa, the latter converging without numerical change to the base of the chamber. Both transverse costae attached to the penultimate costal strips of the longitudinal costae and not directly to the terminal strips forming the spine ends. Apparent length of the anterior spines 15 μm \pm 5 μm , the posterior spine 10 μm \pm 4 μm . Overall lorica length commonly 35 μm \pm 10 μm , with the chamber 12 μm \pm 3 μm but all parts can be either larger under arctic conditions or smaller (southern hemisphere and Galapagos Islands), specimens of the latter type, with an average overall length of 20 μm , perhaps a separate species or subspecies. The number of tentacles approximately 30. Flagellar length variable but can greatly exceed that

of the spines

Geographical distribution probably world-wide in coastal waters. Type specimens collected 19 June 1975 in South Alaska from the sea surface in **mid-channel** about a third of the way between home and St. Augustine Island, water very clean. Also recorded in other samples from the same area at depths from the surface to 10 m and at sea temperatures 6-10°C, also in North Alaska under sea ice (temperature 0°C), in arctic Canada (temperature -1°C), in Britain (temperature 16.5°C), Galapagos Islands (temperature 22°C) and South Africa.

Calliacantha multispina

Original description: Manton and Oates 1979

Lorica 19-34 µm long, lorica chamber (excluding spines) 8-15 µm long. Spines commonly 5 but sometimes 4, 6 or exceptionally 7. Longitudinal costae equal in number to the anterior spines and directly continuous with them (excluding random duplications or deletions affecting single loci). Anterior transverse costa firmly attached to the spines near their lower ends, the posterior transverse costa thinner and more lightly attached near the middle of the longitudinal costae. The component strips of both transverse costae exactly bridging the distance between longitudinal costae. Numerical reduction among longitudinal costae occurring at the hind end of the chamber as in *C. natans*. Distribution, temperate coastal waters near the surface in both the northern (Portsmouth) and southern hemisphere (Cape Town). Type specimen. Specimen in Figure 4 collected 10 November 1972 between Robben Island and Cape Town, 10 m depth, sea temperature 10°C.

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Morphology and distribution of the Acanthoecidae
(Choanoflagellata) from the Weddell Sea during the
austral summer, 1977 / by Kurt Buck. Hanover, N.H.:
U.S. Cold Regions Research and Engineering Laboratory;
Springfield, Va.: Available from National Technical
Information Service, 1980.

vi, 26 p., illus.; 28 cm. (CRREL Report 80-16.)

Prepared for National Science Foundation, by Corps of
Engineers, U.S. Army Cold Regions Research and Engineer-
ing Laboratory, under Grant DPP76-15251 and DPP76-80738.

Bibliography: p. 22.

1. Antarctic regions. 2. Choanoflagellates. 3. Ocean
environments. 4. Plankton. 5. Sea ice. 6. Taxonomy.
I. United States. Army. Corps of Engineers. II. Army
Cold Regions Research and Engineering Laboratory, Hanover,
N.H. III. Series: CRREL Report 80-16.